

GROWTH AND SHELL VARIATION IN THE TROPICAL EASTERN PACIFIC INTERTIDAL GASTROPOD GENUS *PURPURA*: ECOLOGICAL AND EVOLUTIONARY IMPLICATIONS

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ABSTRACT

In this study we investigate variation in shell morphology among *Purpura pansa* Gould, 1853 and *P. columellaris* Lamarck, 1822; high intertidal predatory gastropods found in the eastern tropical Pacific. Field observations on the high frequency of shells intermediate in apertural characteristics, the occurrence of cross-copulations between distinct morph types, coupled with morphometric analyses and examination of sectioned shells lead us to conclude that these two forms are the same species. Hence, we propose *P. pansa* as a junior synonym of *P. columellaris*.

Growth studies reveal that the thicker shelled *columellaris* morph is much slower growing and represents a terminal growth stage of the *pansa* morph. Unlike some other thaidid species, starvation experiments failed to induce thickening of the apertural lip and apertural tooth formation. The stimulus that cues thickening is unknown.

Field experiments indicated that thick-toothed morphs are relatively more resistant to predation and are most common in wave protected, high predation risk environments. Absence of thick-shelled morphs in populations of the geminate congener, *P. patula* in the Caribbean suggests that predation is probably less severe in this region.

INTRODUCTION

Purpura columellaris Lamarck, 1822 and *P. pansa* Gould, 1853 (Family Thaididae), are predatory upper intertidal gastropods common on hard substrates in the tropical eastern Pacific. The northern geographic limit for both species is Baja California (Keen, 1971). Peña (1975) records *P. pansa* from northern Peru; Keen (1971) lists *P. columellaris* further south, from Chile. Both species occur in the Galápagos Islands. *Purpura pansa* is similar to its germinate species in the Caribbean, *P. patula* and previously has been regarded as a subspecies of the latter (Clench, 1947). There is no counterpart of *P. columellaris* in the Caribbean.

The two co-occurring forms are identified by several distinguishing features. The submarginal apertural teeth, a thickened outer lip and a tooth on the columella, characterizes *Purpura columellaris*, whereas *P. pansa* has a thin, often crenulated outer lip and lacks apertural and columellar teeth (Clench, 1947). In Panamá and the Galápagos Islands, one of us (GMW) commonly observed intermediate forms. Lowe (1932) also found intermediate shells.

In this paper we quantify and compare morphometric variation in these two species including a description of the intermediate specimens. Through observations

of copulatory behavior, habitat, growth in the field and the nature of the morphometric variation, we conclude that the thick-shelled, *P. columellaris* is a terminal, but nonobligate slowly growing form of *P. pansa*. Since *P. columellaris* has priority, we propose *P. pansa* as a junior synonym. Second, we provide evidence to suggest that changes in shell shape and growth rate may be an adaptive response to intense predation pressures. Lastly, we speculate on the lack of a thick-shelled growth form for *P. patula*, the Caribbean amphi-species of *P. pansa*.

MATERIALS AND METHODS

Field sites and sampling techniques

Purpura are predaceous thaidid gastropods which live in the mid to upper intertidal zone. Foraging and reproductive activities (*i.e.* copulation and ovipositing) occur in crevices during periods of low water (Garrity and Levings, 1981).

Field work was carried out at two localities: Academy Bay, Santa Cruz Island, Galápagos, Ecuador and the Perlas Islands (Chitre and Saboga), Panamá. Densities and frequencies of shell types were gathered by sampling 0.5 m each side along line transects ($n = 15$, 5–10 m in length) laid out parallel to the shoreline across the high and mid intertidal zones. Size-frequency distributions were collected on shells at the Panamá sites. Shell types were noted, and total shell length measured using vernier calipers.

Frequencies of cross-copulations between individuals with shells typical of *P. pansa* and *P. columellaris*, (*i.e.* excluding intermediates) were recorded at both the Galápagos and Panamá sites over a period of several months. Copulating individuals were temporarily detached from the substrate and shell type and sex were noted. In the Galápagos, copulation occurs in every month of the year, similar to the situation observed in Panamá (Garrity and Levings, 1981).

Shells used in the morphometric analyses (see below) were collected from several islands in the Galápagos. For these analyses an attempt was made to randomly collect shells over a wide range of sizes and shell types.

Morphometric analyses

To evaluate differences in shell shape between these nominate species of *Purpura* we subjected our shells to a principal components analysis (PCA). Prior to measurement each shell was determined to be *P. pansa* or *P. columellaris* according to lip thickness and the presence of teeth. Intermediate shells (Fig. 1) were grouped into three classes based on their similarity to *P. pansa* or *P. columellaris*. Intermediate class one shells were similar to *P. pansa* but laminar deposition had submarginally thickened the apertural lip. Emergent teeth were present on either the apertural lip or the columella. Class two shells had emergent teeth on both the columella and the lip. Class three shells resembled *P. columellaris* but the teeth were not as prominently developed and the last portion of the body whorl was not as heavy as typical *P. columellaris*. Since a complete series of intergrades was available our criteria for distinguishing classes were necessarily subjective.

A sample of 273 shells from the Galápagos Islands were included in the principal components analysis. For each shell, six variates were measured. Length was the distance from the tip of the spire to the anterior end of the shell. Spire height was the distance from the top of the spire to the origin of the suture at the apertural margin. Width was the maximum measurement at a right angle to length along the axis. Apertural length was measured parallel to shell length, and aperture width was

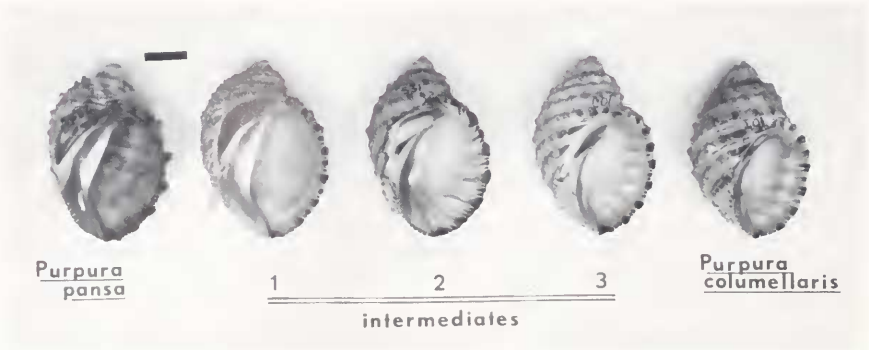


FIGURE 1. *Purpura pansa*, *P. columellaris* and shells of intermediate diagnostic morphology (see text). Dark bar = 1 cm.

the greatest distance from the margin of the outer lip to the columella measured perpendicular to aperture length. Dry weight of the shell was the sixth variable. Linear measurements were taken with vernier calipers to 0.1 mm; weights on an analytical balance to 0.01 g.

For the PCA all measurements were transformed to natural logarithms, and all variates were normalized. These procedures satisfy the assumption of PCA that all samples be drawn from a multivariate, normal distribution (Blackith and Reyment, 1971).

Principal components analysis associates each shell with a point in a 6-dimensional space where each dimension represents one variable. Any line through the origin in this space is a new synthetic variable that gives to any shell a value equal to the distance from the origin to the perpendicular projection of that shell onto that line. The line that removes the most variance is the first principal component (PC I). The line perpendicular to PC I that accounts for the largest remaining variance is the second principal component, and so forth. All six components are uncorrelated. The proportion of the variance subsumed by each component is expressed as an eigenvalue. Interpretation of the principal components is achieved by examination of the eigenvectors. This provides a series of loadings showing the correlation of the original variables with the principal components (Blackith and Reyment, 1971; Kuris and Brody, 1976).

The multivariate statistics indicated that spire height in relation to shell size differed for *P. pansa* and *P. columellaris*. We performed analyses of covariance (ANCOVA) for log spire height on log shell length. For a subset of 20 *P. pansa* and *P. columellaris* we compared spire height with a seventh shell measurement, old spire height, using regression analysis and a nonparametric test of the residuals. Old spire height was the distance from the tip of the spire to the suture of the body whorl 180° opposite the posterior notch of the aperture.

To reveal the history of past growth of these shells, sections were cut with a rock saw. Sections from 25 shells showed the sequential deposition and relative extent of prismatic and laminar shell layers as well as patterns of abrasion and the laminar deposition of shell from the body surface in repair processes.

To test our classification of *Purpura* shells we performed several discriminant functions analyses (DFA) on our morphometric data. A discriminant functions analysis is a very robust multivariate classification procedure because discriminant functions are derived so as to maximize group differences. Examination of the

proportion and nature of misclassifications in the several classification schemes permits us to reject some proposed taxonomic groupings. A discriminant function analysis weights and linearly combines the six shell variables so that the groups identified on an *a priori* basis are forced to be as statistically distinct as possible. Since the initial variables are assumed to be drawn from a multivariate normal distribution, our data were logarithmically transformed and normalized before proceeding with the DFA (Klecka, 1975). Our *a priori* determination of shell group membership used the same combinations of apertural tooth development and lip thickness discussed above. Statistics of the discriminant functions analysis were generated by the SPSS (Statistical Package for the Social Sciences) program (Klecka, 1975). All other statistics were performed with SAS (Statistical Analysis System; Ray, 1979) statistical programs.

Determination of growth rate and starvation experiments

To test the hypothesis that *P. columellaris* represents a terminal growth stage of *P. pansa* we measured growth rates (*i.e.* lateral extension of the outer lip) of *P. pansa* and *P. columellaris*. At the southwest corner of Saboga Island, Panamá, fifteen snails of *P. pansa* (including intermediate class 1) and *P. columellaris* (including intermediate class 3) were marked by file-etching a small groove (2–3 mm deep) into the growing edge of the outer lip. One or more grooves were made on each shell in a unique and identifiable pattern. The animals were released and recovered five months later (26/1/79 to 13/6/79). Extension of the aperture past the groove markings was measured using dividers and a rule.

To test whether starvation could induce shell thickening in *P. pansa*, cages were used to enclose animals *in situ*. Three small cages (20 × 20 × 5 cm) constructed of plastic coated wire frame (2 × 6 cm) and covered with 1 cm wide Vexar® mesh were attached with screws and epoxy to a vertical rock wall within the natural habitat near the interface between the high and mid tide level. One, three, and six *P. pansa* were marked and placed within the three cages respectively. Five *P. pansa* were etched and left outside the cages as controls on adjacent rocks. The experimental period ran from 16/6/79 to 20/11/79.

Predation experiments

To examine the adaptive significance of shell polymorphism we investigated the relative susceptibility of thin (*P. pansa*) and thick (*P. columellaris*) shells to predation. Shells (without animals) were attached with epoxy to open rock surfaces at the high-mid tide interface along both wave-exposed and protected shorelines on Chitre Island, Panamá. Shells were attached during low tides in November 1979 and left for 48–96 hours.

RESULTS

Habitat and population structure

Purpura were most abundant in areas exposed to moderate wave action. Mean population density at the Academy Bay (Galápagos) site was 0.69 individuals/m² (area sampled = 100 m²). Densities were variable; highest (>2 individuals/m²) in or near crevices and under boulders and lowest (0/m²) on exposed flat rock surfaces. Similar results concerning microhabitat distribution have been reported by Garrity and Levings (1981) in Panamá.

Surveys in wave exposed areas indicated that *P. pansa* was the more common species, accounting for 70% of the population (Table I). Ten percent of the snails were intermediate in shell morphology between *P. pansa* and *P. columellaris* (see Fig. 1).

While *P. pansa* was the more abundant species, size frequency data show that *P. columellaris* was significantly larger (Fig. 2: median size = 40 mm for *P. pansa*, 49 mm for *P. columellaris*; $P < .05$ Mann Whitney U-test). A few *P. columellaris* less than 30 mm in length were found during this study (smallest was 20 mm), however, the smaller size classes were predominated by *P. pansa*.

Cross-copulations

Purpura moves out of crevices on falling tides to forage and engage in reproductive activities. During copulation the male climbs onto the shell of the female near the posterior end and inserts its penis into the copulatory bursa located just beneath the mantle (Fig. 3). When disturbed, the penis is withdrawn slowly confirming that copulation actually occurred. In almost all cases males were considerably smaller than females, however, we found no correlation between sex and shell morphology.

Cross-copulations between distinct shell morphs (*i.e.* *P. pansa* \times *P. columellaris*) were not uncommon (Table II) nor were copulations involving intermediate shell forms with one or the other of the distinct morphs (Fig. 3). We have no evidence that these cross-copulations result in viable offspring. Nonetheless, these observations strongly suggest that *P. pansa* and *P. columellaris* are not behaviorally isolated from reproducing. Cross-copulations however, do occur less frequently than expected based on the proportion of *P. pansa* and *P. columellaris* morphs in the population (Table II). Microhabitat differences in the distribution of the morphs may decrease opportunities for cross-copulations.

Morphometric analyses

A covariance matrix for the sample of 273 shells disclosed that all six variables were highly correlated (r ranging from 0.803 to 0.990). Not unexpectedly, the eigenvector of principal component I (Table III) yielded loadings of the shell measurements with PC I that were all highly positive correlations of similar value (r ranging from 0.394 to 0.420). Thus, we interpret PC I to be a synthetic variable representing overall size in accord with other morphometric studies of arrays of similar objects of different size (Blackith & Reyment, 1971; Kuris & Brody, 1976). Most of the variance in the original data set was described by PC I (94.0%). The remaining variance must then be attributed to factors other than size, *i.e.*, aspects

TABLE I

Frequency of occurrence of *Purpura* morphs in the Galápagos Islands, Ecuador and in the Gulf of Panamá, Panamá

Location	N	Thin, untoothed <i>P. pansa</i>	Thick, toothed <i>P. columellaris</i>	Intermediates (1, 2 and 3)
Galápagos	152	103	34	15
Panamá	110	79	22	9
Totals	262	182	56	24
%	—	69%	21%	9%

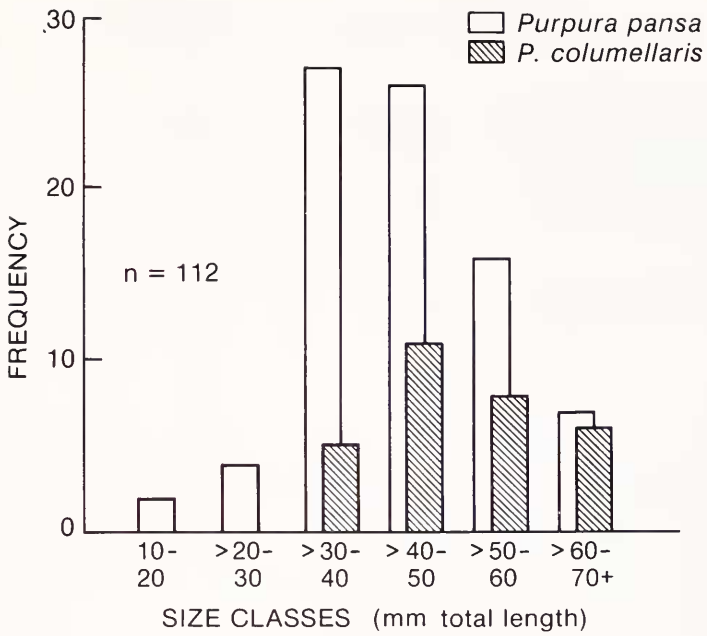


FIGURE 2. Histogram showing the size-frequency distribution of *Purpura pansa* and *P. columellaris* at Chitre Island, Panama.

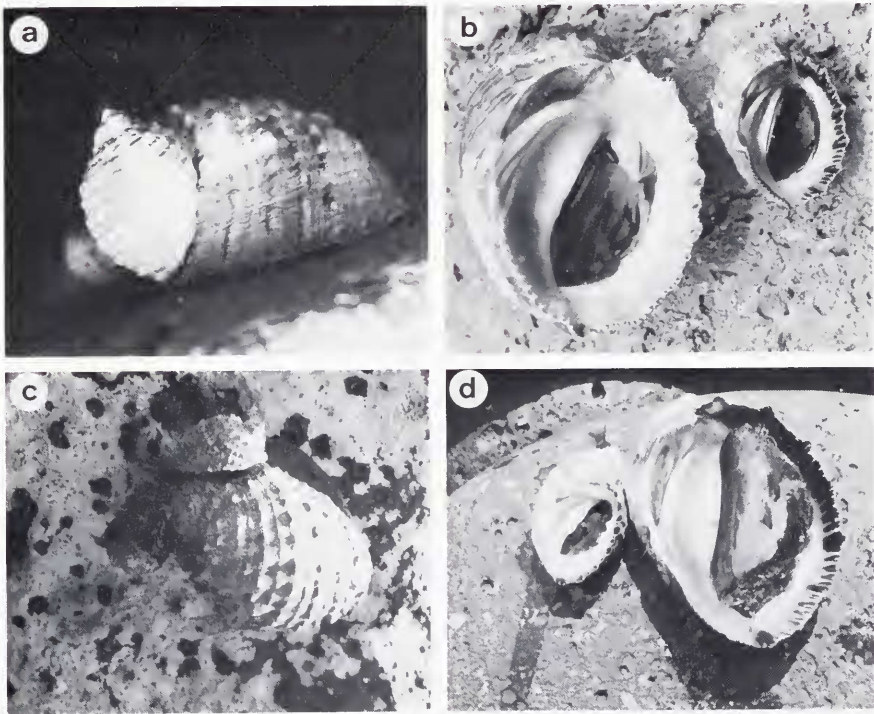


FIGURE 3. Field observations of cross-copulating individuals of *Purpura*. (a) copulation between *P. pansa* (small male) and an intermediate (class 2) morph (large female). (b) same individuals in (a) showing details of shell morphology. Emergent teeth on the outer lip of the aperture and columella are visible in the large female. (c), (d) copulation between *P. pansa* (large female) and *P. columellaris* (small male).

TABLE II

Frequency of copulations observed among and between morphologically distinct snails (i.e. thick, toothed *P. columellaris* and thin, untoothed *P. pansa*) in the Galápagos Islands and at various island locations in the Gulf of Panamá

Location	Total number of copulations	Within-morph matings		Cross-copulations
		<i>P. pansa</i>	<i>P. columellaris</i>	* <i>P. pansa</i> × <i>P. columellaris</i>
Galápagos	52	34	10	8
†Panamá	89	65	13	11
Totals	141	99	23	19
%	—	70	16	13

* Calculated expected frequencies of cross-copulations using the binomial distribution indicate that observed values are significantly less than expected based on the proportion of *P. pansa* and *P. columellaris* in the samples ($\chi^2 = 21.48$, $P < .005$, for Galápagos; $\chi^2 = 32.28$, $P < .005$, for Panamá, see text for discussion).

† A portion of these data represent unpublished observations made by S. Garrity and S. Levings and are cited here with their kind permission.

of shape. Principal component II accounted for 4.6% of the variance and therefore contained most of the information on shape. Spire height and weight gave strong negative correlations and aperture length and aperture width strong positive correlations with PC II (Table III). In visual terms (Fig. 4), shells having a high score on the second component tended to be low spired and light in weight. Their apertures were large (both wide and long). Figure 4 shows that *P. pansa* shells tended to have low spires, light weights and large apertures, whereas *P. columellaris* tended to be heavy, have high spires and small apertures. Thus PCA gives an incomplete separation of *P. pansa* and *P. columellaris*. Most of the intermediate shells do fall between the two species with a gradient along PC II of intermediate class 1 shells falling near *P. pansa* and intermediate class 3 shells positioned near *P. columellaris*. It is also quite evident from Figure 4 that most small shells are *P. pansa* type.

TABLE III

Eigenvectors and eigenvalues (expressed as proportion of the total variance) for the principal components analysis of 273 shells and 6 input variables, and for the PCA of 54 shells over a restricted range of sizes (see text)

Original variables	Principal components (273 shells)		Principal components (54 shells)	
	I	II	I	II
shell length	0.420	0.030	0.508	-0.198
spire height	0.394	-0.612	0.170	-0.589
shell width	0.419	0.136	0.526	-0.069
aperture length	0.413	0.337	0.506	0.272
aperture width	0.402	0.535	0.406	0.472
weight	<u>0.402</u>	<u>-0.454</u>	<u>0.125</u>	<u>-0.595</u>
Eigenvalue (%)	94.0	4.6	49.7	38.0

PC III to VI are omitted as they cumulatively included only 1.2% of the variance in the first analysis.

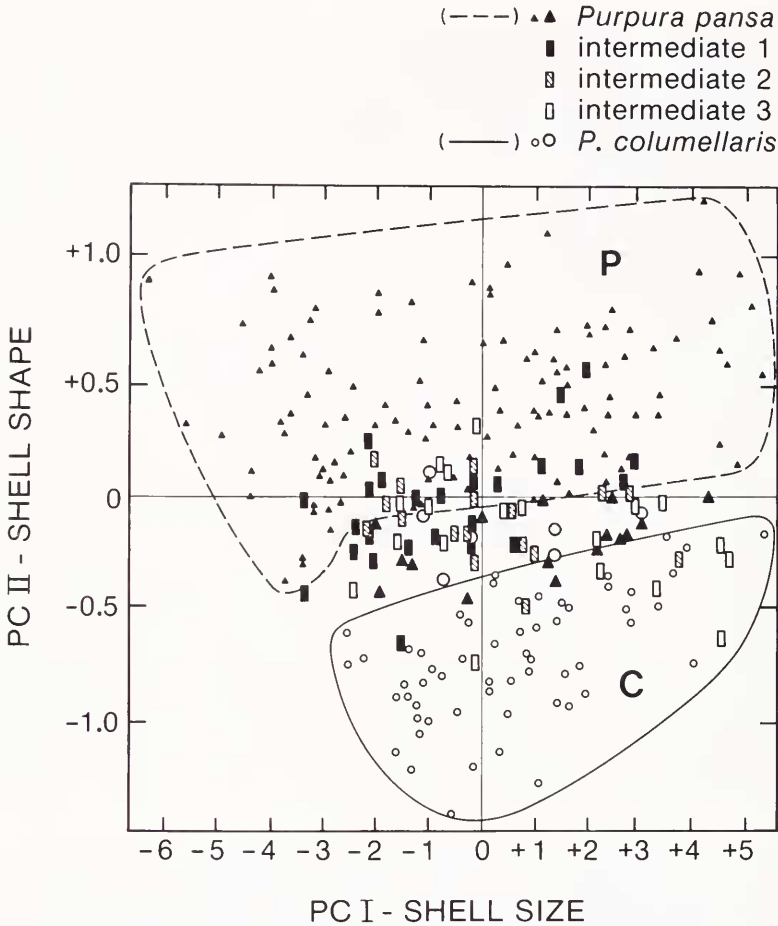


FIGURE 4. Plot of 273 shells used in PCA on the coordinates representing shell size (PC I) and shape (PC II) (see text for interpretation of these axes). All shells identified on the basis of apertural morphology as *Purpura pansa* are indicated by solid triangles and the region occupied by the majority of these shells has been demarcated by the dotted line. All *P. pansa* shells within this zone are designated by small triangles while those located outside the dotted line are indicated by large triangles. Similarly, *P. columellaris* shells are indicated by open circles and a solid line. Intermediate shells of types 2, 3 and 4 (see text) are designated by solid, diagonally shaded and open rectangles, respectively.

To further examine the variance apportioned along the shape components we repeated the PCA using a restricted range of shell sizes. This analysis included all 54 shells within the range of 0.0 to +1.25 on PC I in the original analysis. As Table III shows, the PC I could still be interpreted as a size related variable although spire height and weight now contribute little to PC I. PC II now included a substantial 38.0% of the variance. The loadings on the eigenvector for PC II were generally similar in magnitude and direction to PC II of the 273-shell PCA. Thus, this analysis confirmed that PC II separated shells on the relative dimensions of spire height and weight versus aperture size (both width and length). Examination of plots (not shown) again showed that *P. pansa* tended to have a large aperture, a low spire and are relatively light compared to *P. columellaris*.

Growth model

Field observations on size distributions and cross-copulation between *P. pansa* and *P. columellaris* shells, the presence of numerous shells with intermediate patterns of apertural morphology, and our PCA documentation that these shells intermediate in apertural sculpture were also morphometrically intermediate, suggests that these nominate taxa are growth forms of the same species. We hypothesize that all shells start growth as the *pansa* morph and some selectively thicken the distal portion of the body whorl and develop apertural teeth, thus transforming to the *columellaris* morph. Since no shells were observed to develop in the reverse direction we further propose that this change is unidirectional and irreversible.

Further support comes from an examination of shell sections (Fig. 5). The outer wall of shells with a *pansa* morph has a relatively thin laminar layer secreted by the mantle margin over a thin prismatic layer. The terminal portion of the outer wall (approximately the distal third of the body whorl) of all *P. columellaris* morphs has a thick layer of laminar shell deposited on a thin prismatic layer. However, in the older parts of *P. columellaris* shells only a thin laminar layer is present. The *columellaris* morphs resemble the *pansa* morphs with respect to the relative deposition of laminar material on the outer wall in older parts of the shell. Also evident in Figure 5 is the deposition of a laminar regenerative layer secreted by the mantle surface of the body (rather than by the free mantle surface which produces the laminar layer). This regenerative layer is apparently secreted in response to thinning of the shell due to external abrasion. On the very eroded, oldest portion of the spire this regenerative layer may completely replace the original prismatic and nacreous layers. A similar regenerative shell layer is present in the spire of many prosobranch molluscs. Details of the microstructural components of the regenerative layer has recently been described for *Tegula* by Geller (1982). Observations of sectioned shells

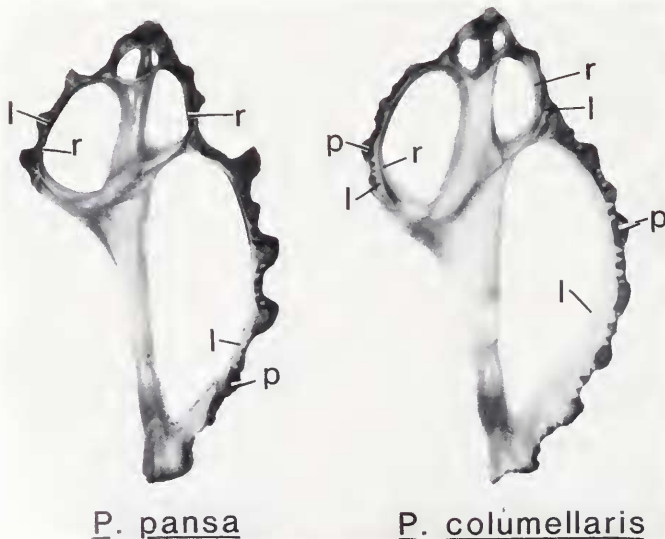


FIGURE 5. Sections of *Purpura pansa* shell (left) and *P. columellaris* shell (right). Sections were cut through the axis of the shell along the columella such that the right-hand side of the shell is about 1–2 mm from the aperture. Both shells were 45 mm long. Shell layers are designated p, prismatic layer; l, laminar layer; and r, regenerative layer.

suggest that increased deposition of this regenerative layer thickens the outer wall of the spire of the *columellaris* morph more extensively than for the *pansa* morph (Fig. 5).

The loadings of the eigenvector of PC II disclosed a morphometric difference between the *pansa* and *columellaris* morphs that had not been suspected *a priori* and suggested a test of this one species-two growth forms hypothesis. The postulated initial *pansa* growth form tended to have a large aperture (both long and wide) and consequently a short spire. This difference in relative spire height was confirmed by an ANCOVA of log spire height on log shell length for shells identified as *P. pansa*, the 3 intermediate classes and *P. columellaris* on the basis of apertural tooth development and body whorl thickness. No significant differences were found among slopes for all 5 shell types. Intercepts of both *pansa* and *columellaris* morphs were significantly different from each other and from all three intermediate classes. Grand means of the *pansa* morph had significantly lower spire heights than did the *columellaris* shells.

If growth proceeds to a *columellaris* morph, the aperture must exhibit a relative decrease in allometric growth resulting in a relatively high spire since aperture length and spire height are inversely proportional measurements. Thus, a measurement of former spire height taken at a sufficient distance before the aperture along the body whorl of the *columellaris* morphs should be relatively small compared to the present spire height if growth of the aperture length of these shells has not kept pace with growth of the rest of the shell. In contrast, the old spire height of the *pansa* morph should be similar to the present spire height as a relative proportion of shell size. For this comparison we selected an old spire height 180° opposite the aperture. If the relative change in spire height is confirmed for the *columellaris* morph, this would further indicate that the change from the *pansa* to the *columellaris* morphs occurs over less than one half of a whorl and therefore that the *columellaris* morphs grow very slowly, if at all, once the transformation is complete. Present spire height of the *columellaris* shells is high relative to the old spire height (Fig. 6). All of the log-transformed values for previous versus present spire height in *P. columellaris* fall above the regression line for the *pansa* shells. This difference is significant (X^2 , $P < .01$). A comparison of the *columellaris* and *pansa* old spire height-present spire height is permissible since the analysis of covariance of present spire height on shell length showed that allometry of the slopes was very similar (0.927 for *pansa* and 0.889 for *columellaris*, $P > .25$).

Classification tests

Principal components analysis and regression statistics support the hypothesis that *pansa* and *columellaris* morphs are growth forms of the same species. The intermediate shells represent specimens in the process of transforming from the former to the latter morph. Classification procedures in the discriminant functions analysis were used to inspect and test this as well as competing hypotheses. The first classification (Table IV) was based on a discriminant function that strongly separated shells determined on the basis of apertural teeth and lip thickness to be *P. pansa* and *P. columellaris*, respectively. Over ninety-nine percent of these shells were successfully discriminated by this procedure. However, when this discriminant function allocated the intermediate shells, 58 percent were assigned to *pansa*, 42 percent to *columellaris*. This relatively even split would be expected if the intermediate shells represented a continuum from *pansa* to *columellaris*. Further support for this interpretation of the intermediate shells would be gained by a high likelihood of

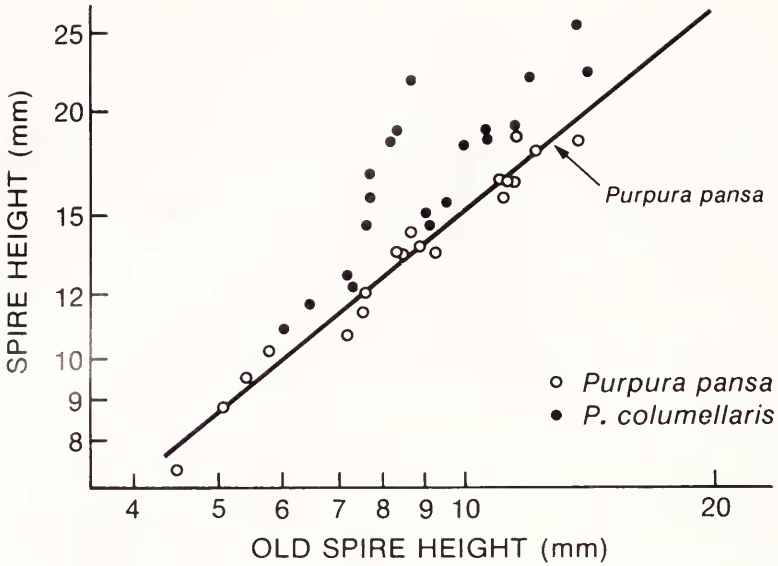


FIGURE 6. Relationship between log old spire height and log spire height (see text for definitions) of 20 shells identified as *Purpura pansa* (open circles) and *P. columellaris* (closed circles) on the basis of apertural morphology. The regression line was fitted to the data for *P. pansa* only to show the relative increase in spire height of *P. columellaris* following the growth of one-half of a body whorl.

misclassification. Such was reflected by a low probability ($<.05$) of being located as far as they were from either centroid. By this criterion, 48% of the intermediate shells could not be reliably classified.

TABLE IV

Discriminant functions analysis classification of shells following assignment of shell to predicted shell groups on the basis of apertural teeth and lip thickness

DFA	<i>a priori</i> classification	Percentage of shells correctly classified	Percentage of shells misclassified as		
			P	I	C
1	P	99	—	—	1
	C	100	0	—	—
	ungrouped I*	—	58	—	42
2	P	87	—	12	1
	I	79	13	—	8
	C	92	0	8	—
3	P + I†	93	—	—	7
	C	98	(2)	—	—
4	P	97	—	—	(3)
	C + I†	88	12	—	—

P = *Purpura pansa*, I = intermediate, C = *P. columellaris*.

* In the first DFA the intermediate shells were not grouped and the classification procedure assigned each shell to either P or C based on their loadings on the discriminant function.

† In the third and fourth DFA, intermediate shells were combined with either P or C. Numbers in parentheses refer to the percentage of shells misclassified into the combined categories.

The second DFA tested the hypothesis that the intermediate shells represented a third taxon, distinct from either *pansa* and *columellaris* and about 10 per cent of each of these latter shell types were misclassified as intermediate. This pattern is not consistent with a hypothetical third type that is not intermediate.

The third and fourth DFAs jointly examine the possibilities that either *P. pansa* or *P. columellaris* are variable species with the intermediate shells being either "toothed" *P. pansa* (first hypothesis) or "smooth" *P. columellaris* (second hypothesis). Thus, a DFA was performed to separate *pansa* plus the intermediates from the *columellaris* shells (Table IV). Here a high degree of separation was achieved with only 5.5% of the shells misclassified. However, the same degree of separation was achieved in the reverse analysis (*columellaris* plus intermediates versus *pansa*) since only 7.7% were misclassified. Taken together, these tests enabled us to reject both of these "variable species" hypotheses.

Growth rates

Results from the morphometric analyses suggest that *P. columellaris* is a terminal growth form of *P. pansa*. This hypothesis predicts that the former morph should be slower growing than the latter. Growth measurements recorded at Saboga (Panamá) appear to confirm this prediction (Table V). Using similar sized snails, the apertural lip of *P. pansa* grew twice as fast as that of *P. columellaris* ($P < .01$, Mann Whitney U-test).

Starvation experiments

There is some evidence that thickening can be induced by stress such as starvation, in other thaidids (Bryan, 1969; Cowell and Crothers, 1970). Results from our enclosure experiments using *P. pansa* morphs indicate that at least severe starvation is not an important stimulus for shell thickening. We found no evidence of tooth formation among our experimentally caged snails. The apertural lip in several animals, however, had become quite worn. Shell morphology of all the control animals remained unchanged throughout the experiment.

Considering the slow growth of *Purpura* and the complete starvation conditions of our experiment we cannot reject the starvation hypothesis with confidence. It may be that chronic or periodic rather than complete starvation induces shell thickening.

Predation experiments

The distribution of *Purpura pansa* and *P. columellaris* generally overlap but often differ quantitatively depending on exposure to wave action. For example, at

TABLE V

Linear growth of the outer lip of Purpura pansa and intermediate class 1 versus P. columellaris and intermediate classes 2 and 3 from 23 January 1979 to 15 June 1979 at the southwest corner of Saboga Island, Gulf of Panamá

Shell form	Sample size	Total shell length (mm)	Linear growth of the outer lip after five months (mm)
<i>P. pansa</i> + intermediate 1	10	41.7 (± 12.35)	2.7 ($\pm .65$)
<i>P. columellaris</i> + intermediates 2 and 3	5	41.5 (± 8.25)	1.4 ($\pm .55$)

Values represent means with standard deviations in parentheses.

Chitre Island (Panamá) we found that in wave exposed situations (southern shore) 76% of the *Purpura* population was composed of *pansa* morphs while only 14% were *P. columellaris* and 10% intermediates ($n = 99$). Conversely, in protected area (northern shore) *Purpura* were much less abundant but were predominantly *P. columellaris* (73% *P. columellaris*, versus 27% *P. pansa*: $n = 11$).

Using tethered *Purpura* Garrity and Levings (1981) found that within a 24 hour period fish predation resulted in 25% mortality. Results from our experiments, placing thick (*P. columellaris*) and thin (*P. pansa*) shells in wave exposed and protected areas, reveal that thick shells were more resistant to shell breakage than were thin shells, particularly along protected shorelines (Table VI: on wave exposed shores difference in shell damage between thick and thin-shelled morphs was not significant, $P > .05$, but on protected shores thin-shelled morphs suffered significantly higher damage, $P < .01$, Fisher's Exact Test).

Because characteristic fused-tooth marks were found on the surfaces of several unbroken thick shells, we suspect that pufferfish (*Arothron* spp. and *Diodon* spp.) were responsible for most of the experimentally observed shell damage. Garrity (pers. comm.), however, has pointed out to us that crab predation may be an even greater source of differential mortality among *Purpura* shell morphs. Thickening of the apertural lip in gastropods has been shown to reduce successful predatory attacks by crabs (Vermeij, 1978).

DISCUSSION

Field observations on the high frequency of shells intermediate between *Purpura pansa* and *P. columellaris* in apertural characteristics, numerous observations of cross-copulation between these types, inability to locate very small *P. columellaris* in the field (or in museum collections), when coupled with our morphometric analyses and shell sections, strongly suggest that these two long recognized taxa are the same species. Thus, we propose that *P. pansa* Gould, 1853 is a junior synonym of *P. columellaris* Lamarck, 1822.

The *columellaris* morph of *P. columellaris* appears to be a facultative terminal growth form. All shells initially grow as the *pansa* morph. Transformation to the *columellaris* morph can occur over a very wide size range. This change includes the development of columellar and submarginal teeth in the aperture. The apertural lip

TABLE VI

Results of predation experiments on *pansa* and *columellaris* morphs in the mid-intertidal zone at Chitre Island, Panamá

Situation	Shell morph	Sample size	Mean total length-mm (range)	Number of shells damaged (%)	†Significance level
exposed (southern shore)	<i>pansa</i>	31	42.1 (35.7–48.7)	3 (9.6%)	$P > .05$
	<i>columellaris</i>	17	42.3 (36.1–51.5)	0 (0)	
protected (northern shore)	<i>pansa</i>	33	41.4 (35.0–47.1)	17 (51.5%)	$P < .01$
	<i>columellaris</i>	20	43.8 (33.6–51.0)	2 (10.0%)	

Experiments ran 48–96 hours.

† Fisher's exact test.

thickens. Linear growth rate decreases. Increased laminar deposition thickens the outer wall of the younger portion of the body whorl and increased regenerative layer deposition thickens the older portion of the shell. As the transformation proceeds, the relative growth of the aperture decreases to produce a high spired, small apertured shell. Transformation from the *pansa* to the *columellaris* morph is completed over the growth of less than half a whorl. The process appears irreversible since shell sections never disclosed early periods of tooth formation or increased laminar deposition on the shell wall. The *columellaris* morph probably grows very slowly since old spire height measurements were always relatively small. Vermeij (1980) also reports a strong inverse correlation between spire height and shell growth rates. Observations on growth in the field suggests that the *columellaris* shells are growing slower than *pansa* morphs of the same size. Growth of the *columellaris* shells did not cease since prismatic shell deposition was still evident at the apertural margin.

The only counter evidence to this evaluation is the record of *P. columellaris* from Chile (Keen, 1971). If this species is merely a facultative terminal growth form then its geographic range must be inclusive of the range of initial *pansa* growth form. Examination of extensive new material at the Los Angeles County Museum (LACM) reveals that *P. pansa* occurs south to Islas Lobos de Afuera, Peru, a record south of the locality, Piura, listed by Peña (1975) in his extensive checklist of Peruvian molluscs. Peña (1975) did not list *P. columellaris* from Peru. At LACM the southernmost collections of *P. columellaris* was La Libertad, Ecuador, where it occurred with the *pansa* morph. Finally, McLean (pers. comm.) who has collected extensively along the western coast of South America states that neither species occurs in southern Peru or Chile. Based on this new information the geographic data are consistent with our one-species, two growth form analysis. The record in Keen (1971) may be in error.

The development of apertural teeth during periods of starvation and slow growth has been reported for another thaidid gastropod, *Nucella lapillus* (Cowell and Crothers, 1970; Crothers, 1971). However, in this species the process is reversible. When conditions improve, relatively rapid growth is resumed and teeth are no longer secreted along the apertural margin. In these shells the presence of teeth inside the aperture marks past periods of slow growth. A similar pattern has been observed by AMK (pers. observ.) for *Acanthina punctulata* and for *N. lamellosa* by Spight *et al.* (1974). Temporary periods of arrested linear growth are associated with the development of thick ribs, varices and complex apertural sculpture in many snails (*e.g.* muricids, cassids, cymatiids) (MacKenzie, 1961; Laxton, 1970; Spight, 1973; Spight *et al.*, 1974). *Rissoa parva* exhibits a seasonal tendency to alternate between ribbed and smooth shell morphs (Wigham, 1975). In other snails growth ceases and a terminal morphology develops that typically includes increased laminar deposition forming a thickened apertural lip. Termination of growth is often obligatorily associated with the onset of sexual maturity. Examples include cypraeids, aporrhoids, cymatiids, strombids, helicids and *Cerithium nodulosum* (Randall, 1964; Laxton, 1970; Spight *et al.*, 1974; Pollard *et al.*, 1977; Yamaguchi, 1977; Kat, 1981).

The relationship between the morphs of *Purpura columellaris* has some relatively unusual features. The transformation is not reversible. It is not necessarily associated with sexual maturation and it is not obligatory. As indicated in Figure 4, switch to the *columellaris* morph occurs over a very wide range of sizes [as Yamaguchi (1977) shows also for *Cerithium nodulosum*] and many large specimens of the *pansa* morph are sexually mature. It remains to be confirmed whether sexually immature *columellaris* morphs exist. The cue for the transformation is presently unknown.

Variation in shell sculpturing and morphology has been postulated to be a response to one or more environmental conditions (Moore, 1934, 1936; Phillips *et al.*, 1973; Spight, 1973; Kitching and Lockwood, 1974; Wigham, 1975; and others). Evidence has been found for some species to indicate direct genetic control of variation and that patterns of distribution reflect differential mortality or habitat selection (Struhsaker, 1968). Little is known about the reproductive biology of *Purpura* except that S. Garrity and S. Levings (pers. comm.) have found gelatinous egg masses. We examined several small shells (<10 mm total length) and found evidence of an embryonic shell (protoconch I) occupying the first whorl and a second protoconch extending an additional one to two whorls. The presence of the second protoconch indicates a pelagic juvenile stage (Jablonski and Lutz, 1980). Thus, it is probable that at least a portion of the larval development is planktonic and dispersal widespread.

Because there appears to be some degree of nonrandom distribution and non-random copulations between morph types, it is possible that selection could act to fix these shell characters. However, given microhabitat variability, temporal variation in wave exposure conditions, and evidence for a juvenile planktonic stage, we suspect that shell thickening may be a phenotypic response to environmental conditions.

Ecological and evolutionary implications

Our predation experiments unequivocally demonstrate that the thick *columellaris* morph is relatively more resistant to predation by shell-crushing organisms. Analogous results have been shown for temperate thaidids and littorinids (Kitching *et al.*, 1966; Kitching and Lockwood, 1974; Raffaelli, 1978; Dudley, 1980; Vermeij, 1982). Kitching *et al.* (1966) found that thick forms of *Nucella* predominated along wave protected shores where crab densities were high. Experiments in the laboratory and field showed significantly higher mortality by crab predation among thin compared to thick shells.

Predation rates appear to be low along exposed shorelines perhaps because predators may have a more difficult time negotiating in a high energy environment where swift currents and low visibility could reduce effective foraging. Thin shells therefore may have a refuge from predators in such habitats.

What potential advantage might thin-shelled morphs have over thick-shelled counterparts? Work by Kitching *et al.* (1966) demonstrated that thin-shelled snails were better able to adhere to the substrate, especially where wave action was strong. We have found thick *columellaris* shell morphs more easily dislodged from rocks than thin-shelled *pansa* morphs. The wider aperture and lower spire of the *pansa* morph permit a greater surface area for pedal adhesion. The shells of *Purpura* from very exposed situations tend to be nearly as wide as long giving them a limpet-like appearance. Such animals are extremely difficult to dislodge by hand.

Variation in shell morphology among eastern Pacific *Purpura* may represent an adaptive response to two different and opposing selective pressures; thick shells may be favored where predation risk is high (*i.e.* wave protected shores) and thin shells in environments subject to high wave action but lower predation. The absence of complete segregation of morph types probably reflects the spatial variability in these microhabitats. Snails on the lee sides of large boulders in wave exposed areas are potentially accessible to fish predation.

Since the appearance of the Panamanian isthmus three million years ago (Keigwin, 1978), *P. columellaris* in the eastern Pacific has diverged morphologically while

P. patula has remained conservative: there is no equivalent thick morph counterpart in Caribbean populations. Although, heavy high-spined *P. patula* with thick outer lips are occasionally recovered, these specimens lack any evidence of tooth development (Vermeij, *in litt.*). This dichotomy may be due to differences in predation intensity between oceans. Major differences in shell architecture and ornamentation among gastropod taxa in different oceans have been argued to represent adaptations to gradients in predation intensity (Vermeij, 1976). Laboratory experiments have shown that when eastern Pacific fish (*Diodon* spp.) were presented with eastern Pacific and Caribbean congeners of closely related gastropod species they were able to crush and consume larger-sized Caribbean forms, indicating that snails from this region are less predator resistant (Palmer, 1979 and Palmer cited in Vermeij, 1978 p. 123). Using empty shells in a controlled field experiment, Glynn (unpubl. data) found that the eastern Pacific corallivore, *Jenneria* was heavily preyed on in the eastern Pacific but largely ignored in the Caribbean. Finally, fish predation on hermit crabs occupying gastropod shells was shown to be much greater along the Pacific coast of Panamá than on the Caribbean side of the isthmus (Bertness, 1982).

In addition to faunal differences between oceans, one possible explanation for the apparent low predation rates in the Caribbean, especially for intertidal species, is the small tidal amplitude. In the Bay of Panamá tides fluctuate *ca.* 7m but on the Caribbean side it is less than one meter (Glynn, 1972). Hay (pers. comm.) notes that in the Caribbean herbivorous fish are largely excluded from the shallow reef-flat. Possibly predatory fish are also excluded from shallow rocky intertidal areas.

In conclusion, the isolation of conspecific *Purpura* following the appearance of the Panamanian isthmus three million years ago provided a unique natural experiment. The results support Vermeij's hypothesis that interoceanic differences in gastropod shell morphology represent an evolutionary response to differences in predation pressures.

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